

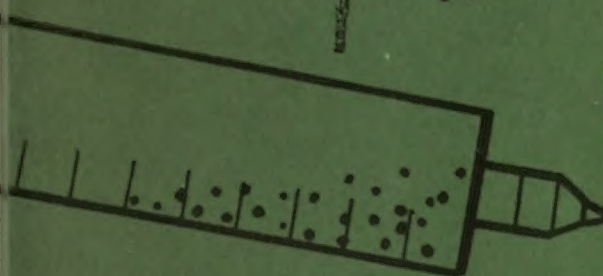
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GENETICS

of RED PINE



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This publication is one in a series on the genetics of important forest trees of North America published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and by the Fifth World Forestry Congress in Seattle, 1960. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

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The Genetics of Red Pine

D. P. Fowler¹ and D. T. Lester²

INTRODUCTION

Red pine (*Pinus resinosa* Ait.) is apparently an old species. Fossils about 100 million years old from southern Minnesota contain a species, *P. clementsii*, markedly similar to the present species (Chaney 1954). Survival during several glacial advances was accomplished presumably by southern migration of the species and subsequent reinvansion of areas vacated by retreating glaciers.

Pollen diagrams suggest that red pine survived the most recent glaciation in a refuge in the Appalachian Highlands and then migrated west, principally north of Lake Michigan (Wright 1964a).

Red pine in the Great Lakes States and Ontario apparently reached its most recent peak of successional stability during an hypothesized hypsi-thermal period between 5,000 and 3,000 years ago. Less frequent fires and a gradual trend toward cooler climate now restrict stable populations to drier areas of the range.

Haddow (1948) characterized red pine as a decadent and retreating species within 100 miles of its northern limit in Ontario. Fowler (1964a), while agreeing that stands near the northern limit are remnants, noted that retreat was more a question of changing habitat than the results of inbreeding as suggested by Haddow. Cook, Smith, and Stone (1952) discussed the persistence of red pine in New York where the species has existed at nearly all reported locations over the last 250 years. The authors noted, however, that few of the New York populations appeared to be expanding. Horton and Bedell (1960) suggested that many stands are edaphic or pyric relics.

The current natural range was depicted in detail by Critchfield and Little (1966). The commercial range was outlined by Rudolf (1957). These distributions are combined in figure 2.

Rock outcrops, lacustrine clays, and windblown



Figure 1.—After fourth thinning, this outstanding 50-year-old plantation at Star Lake, Wis., produced 69 cords per acre. (Photo by Wisconsin Conservation Department.)

sands support natural stands although commercial forests are most commonly found on terrace and outwash sand plains. Sites occupied by succession-

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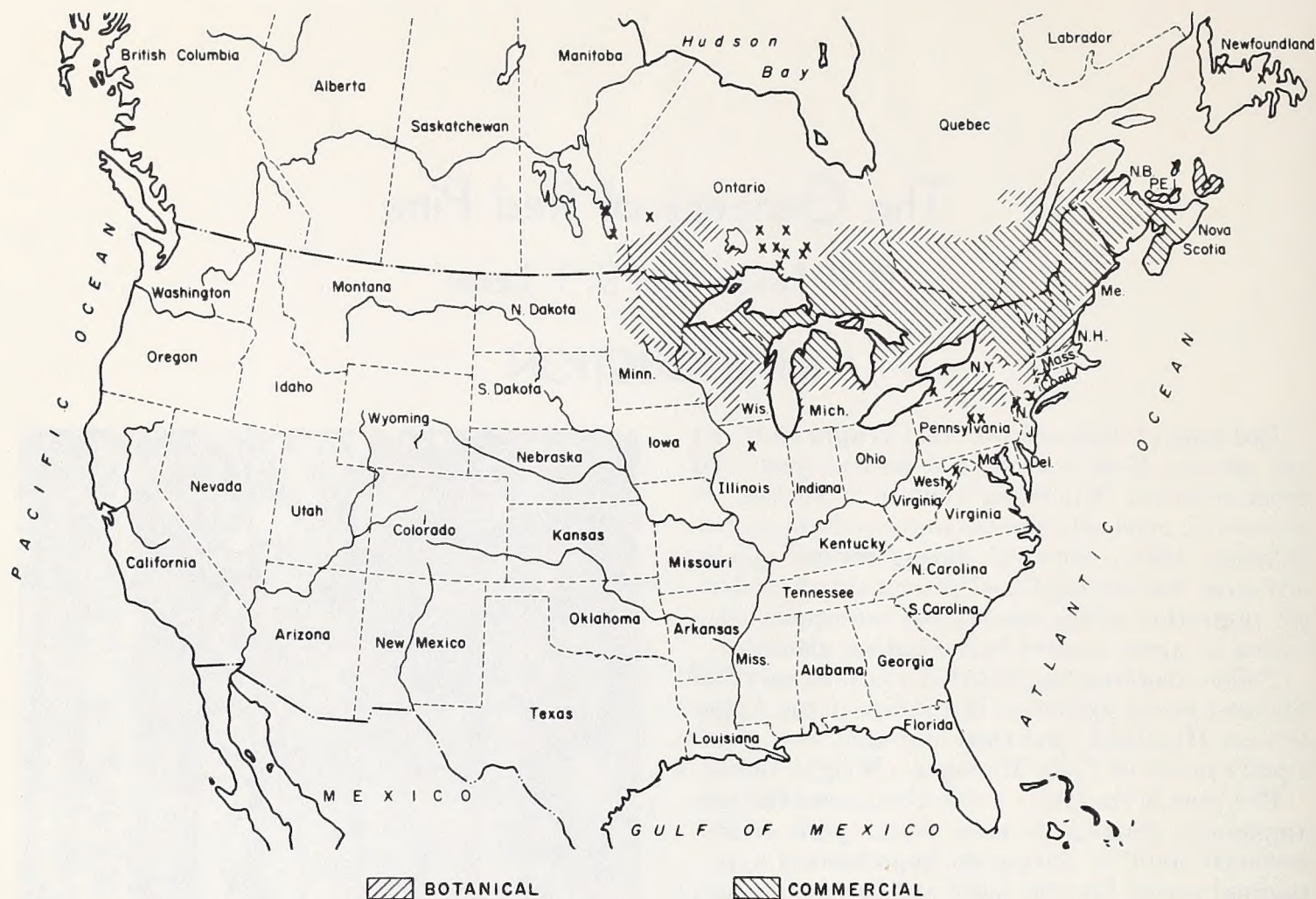


Figure 2.—Ranges of red pine according to Critchfield and Little (1966, botanical) and Rudolf (1957, commercial).

ally stable populations reflect the relatively limited ability of the species to compete with overstory and ground vegetation. The deep, widespread root system of red pine facilitates adaption to coarse, acidic, well-drained soils.

Predominantly a fire species, red pine establishes best on mineral soil. Suitable seedbeds may exist for only a short time (Cook et al. 1952), and in many areas, absence of fire may preclude adequate site conditions for natural regeneration. Also, its periodic seed production and the inability of seeds to remain viable for long periods places red pine at a competitive disadvantage with more fecund associates.

Within the natural range, the frost-free period varies from 60 to 180 days although frost may occur in any month at some locations (Boughner, Longley, and Thomas 1956). Frost damage during flushing may be important in plantation establishment. Frost damage has been noted throughout the growing season on first-year seedlings in natural populations (Horton and Bedell 1960). Precipitation during the frost-free period ranges from 15 to 25 inches and snowfall from 40 to 150 inches

(Rudolf 1957). Altitudinal distribution is generally between 500 and 1,500 feet, although natural populations in New York reach 2,300 feet (Cook et al. 1956) and an outlier in West Virginia ranges from 3,800 to 4,300 feet (Buell 1940).

The decreasing successional stability of red pine in contemporary climate is not reflected in use of the species for artificial regeneration. Annual nursery production of red pine in Wisconsin has exceeded 15 million trees for the last 15 years (Anonymous 1966). Ease of nursery culture and plantation establishment, relative freedom from insects and disease in most areas, and high productivity on suitable sites are major reasons for popularity of red pine for planting.

Plantation growth in Wisconsin has been surveyed in detail by Wilde et al. (1965). Highest productivity is expected on sandy to loamy soils with good drainage and ground water within 9 feet of the surface. Nutrient requirements are low, but vary in relation to other site conditions.

Commercial forests of red pine are confined within the natural range, although moderate growth rates have been reported for trees planted

in Kansas,³ Washington (Silen and Woike 1959), and New Zealand (Sweet 1963). By contrast, high mortality in seedbeds and field planting characterize provenance experiments in Western Europe. Holst (1960) interpreted these losses as indicative of narrow ecological amplitude.

Red pine typically produces one shoot annually from a bud that is fully differentiated in the preceding season (Duff and Nolan 1958). Shoot elongation is rapid, being largely completed within 6 weeks after flushing in May. Lammas

growth may be frequent in young trees but seems to have no effect on total shoot elongation (Rehfeldt and Lester 1966). Patterns of early height growth in plantations are largely exponential up to ages 4 to 10, and then become linear at least to age 25 (Horton and Bedell 1960; Lester and Barr 1966). Early growth patterns, however, can be strongly influenced by competition with ground vegetation and by depth to water table (Wilde et al. 1965). Rotation ages commonly range from 80 to 140 years depending on site and utilization.

SEXUAL REPRODUCTION

Reproductive Development

Red pine is a monoecious species. It occasionally reaches sexual maturity at from 5 to 12 years of age, but under natural conditions seed production does not begin until about 20 to 25 years even on open-grown trees (Woolsey and Chapman 1914). Righter (1939) reported that red pine produced ovulate cones at 5 years and pollen at 9 years at Placerville, Calif. Observations by the writers indicate that, under normal conditions, ovulate cone production begins a few years earlier than pollen production. Attempts to decrease the age-to-flowering by use of cultural treatments such as girdling, root-pruning, bud-pinching, and fertilizers have been unsuccessful with juvenile red pine (Holst 1961). Cone production in mature red pines can be influenced by girdling, strangulation, artificial drought, and fertilizers (Holst 1961; Hitt 1964). Holst (1961) considered that treatments that increase tree vigor (especially fertilization with ammonium nitrate) increase ovulate cone production in mature red pine.

The time scale of cone morphogenesis was studied cytologically by Duff and Nolan (1958). Cone initiation in south-central Ontario apparently occurs in July and August. Cytological evidence (loc. cit.) and results from girdling experiments (Holst 1962) indicate that staminate cone primordia are initiated in July. Buds containing partially differentiated staminate cones are recognizable in autumn by their markedly greater diameter in relation to length. Differentiation of the staminate cone is more advanced in autumn than the ovulate cone. Duff and Nolan (1958) were able to recognize ovulate cone primordia first in late August. Buds containing ovulate cone primor-

dia occasionally can be identified by touch in autumn although differentiation proceeds throughout winter. Visual identification of ovulate cones is not reliable until the buds begin to emerge.

Anthesis occurs in May or June depending on the locality and year. In the Lake States and southern and central Ontario, anthesis usually occurs between mid-May and mid-June. At the northern limit of the species range, anthesis may be 3 to 4 weeks later (Fowler 1965b).

Staminate cones appear in clusters around the basal part of elongating shoots in the lower crown. Ovulate cones, ranging from one to eight per shoot, are first visible as completely enclosed buds adjacent to the shoot apex on elongating shoots in the upper crown. The red cones push through the enclosing bud scales within a week or two. As the cone emerges, the ovulate scales become perpendicular to the cone axis thus marking the period of maximum receptivity. Lyons (1956a) found that ovulate cones contain from 30 to 110 ovules depending on size and position in the tree crown. However, the proximal parts of the cone are barren or have a reduced number of ovules.

Pollination is usually a prerequisite of cone development, and fertilization is necessary for the production of viable seeds (Fowler 1965b). Pollination is normally by wind. Pollen dispersal distances have not been reported. Within 3 to 5 days following maximum receptivity, the ovulate scales close to form a compact, purple conelet.

Cytological observations of development following pollination have been presented by McWilliam (1958) and McWilliam and Mergen (1958). Development follows the pattern typical of pines with fertilization occurring about 13 months after pollination. Although no information is available on the frequency of multiple fertilization and polyembryony for red pine, multiple seedlings have been observed with a frequency of about 0.5 per-

³ Correspondence with P. L. Roth, Department of Forestry, Southern Illinois University, Carbondale, Ill., Jan. 8, 1969, on file at Department of Forestry, University of Wisconsin, Madison, Wis.

cent among germinating red pine seeds.⁴ Usually only one seedling is completely developed; the others are small and usually fail to survive.

The cones rapidly increase in size during late spring and early summer. By late August, a change from green to purple color and a lowered specific gravity mark cone maturity. Cones are considered ripe when specific gravity reaches 0.80 to 0.94 (anonymous 1948). Cones become brown and shed most of their seeds by November.

Good cone crops are produced at intervals of 3 to 7 years with light crops in most intervening years (anonymous 1948). Annual variation in the numbers of ovulate cones initiated (Duff and Nolan 1958), ovule abortion (Lyons 1956a), losses of 1-year-old cones from undetermined causes (Lester 1967), insect damage, and squirrel damage are major factors in periodicity of mature cone crops. In northern Wisconsin, the relative magnitudes of the crop of first-year cones and the subsequent crop of second-year cones were similar and cone crop size was highly correlated with temperature at the time of, or prior to, cone initiation (Lester 1967). Prediction of cone crops several months in advance is possible.

Cone production in red pine plantations has been responsive to cultural treatments. Reduced stand density and increased soil fertility have markedly increased numbers of cones on trees at age 25 (anonymous 1965). Estimates from older trees in stands unmanaged for seed production (Rudolf 1962) suggest that the average annual seed production from 500 trees or less in seedling seed orchards may be adequate for nursery production of 1 million seedlings.

The number of viable seeds per cone averages about 20 and varies from 14 to 60. Seed production in mature red pine stands ranges upward to 110,000 seeds per acre in moderately heavy seed years (Shirley 1933). Cleaned seed averages between 52,000 and 55,000 per pound and ranges from 30,000 to 71,000 (anonymous 1948; Ontario Department Lands and Forests 1958). Under natural conditions, cones open on hot, autumn days when there is little wind to carry the seed far (Rudolf 1957). Although seeds may be disseminated up to 900 feet (Woolsey and Chapman 1914), the effective range is not much more than half of tree height (Rudolph 1957).

Insects and rodents often play an important role in determining the success of red pine seed crops. The red squirrel, *Tamiasciurus hudsonicus*, (Erxleben) often collects red pine cones, and sev-

eral other rodents and birds eat large quantities of the seeds that reach the ground (Rudolf 1957). Several insects may reduce red pine seed crops. The red pine cone beetle, *Conophthorus resinosae* Hopk., may destroy virtually entire red pine cone crops over large areas (Lyons 1956b). For detailed description of insects that damage red pine cones, the reader is referred to a series of papers by Lyons (1956b, 1957 a, b, c).

Cross- and Self-Pollination

In closed stands or in plantations, red pine is a cross-fertilizing species. Under these conditions, Fowler (1965b) estimated that no more than 10 percent of the seeds result from self-fertilization. On the other hand, a high proportion of seeds from isolated trees or from small groups of trees result from selfing. In most red pine trees a fairly large area of the crown carries both staminate and ovulate cones. Crown form has a definite effect on this area of overlap. Separation of the sexes is most definite in trees growing in closed stands or plantations. In open-grown trees or in trees which have had their tops damaged, separation of the sexes is poorly defined. Vertical separation of the staminate and ovulate cones appears to be the most important factor limiting self-pollination. Cones collected from the lower portion of a tree crown contained almost twice as many selfed seeds as cones from the upper tree crown.

Dichogamy does not appear to be a barrier to self-pollination in red pine. Pollen shedding usually begins about the time that ovulate cones become receptive and continues throughout the receptive period. Red pines from nine climatic regions, growing in a provenance test at Kane, Pa., were synchronized to within 2 days in respect to onset and conclusion of pollen dispersal and stages of ovulate cone development. As much variation in cone development was observed within single trees as between trees of widely different origins.

Although red pine is monoecious, in years of average or poor ovulate cone production almost all codominant and dominant trees produce an abundant pollen crop. Thus, many trees are functionally male. The presence of a large number of pollen producing trees probably results in less selfing than if pollen were produced only on trees bearing ovulate cones.

Selective fertilization, the favoring of outcrossing over selfing, does not appear important in red pine. However, selection against a deleterious recessive mutant has been shown to take place during the period between pollination and seed germination (Fowler 1964b).

⁴ D. P. Fowler, unpublished data on file, Department of Fisheries and Forestry, Fredericton, New Brunswick, Aug. 15, 1967.

Controlled Pollination

Techniques used for controlled pollination of red pine are basically the same as those reported by Cummings and Righter (1948), Mergen, Rossol, and Pomeroy (1955), and Wright (1962) (fig. 3). Many workers have modified these techniques to suit local conditions. Most modifications have been of isolation bags, pollen extractors, pollen applicators, or marketing techniques.

Red pine pollen can be collected a few days prior to normal pollen shedding. A good rule of thumb is that once the exudate from squeezed staminate cones is yellow, the pollen is mature enough for collection. Almost any drying method that prevents contamination and does not subject the pollen to extremes of temperature is satisfactory. Sausage casing extractors (Wright 1962) are useful for



Figure 3.—Controlled pollinations being made in the crown of a selected red pine at Baskatong Lake, Province of Quebec (Photo by Department of Fisheries and Forestry, Petawawa Forest Experiment Station, Chalk River, Ontario.)

field extractions. The pollen usually is separated from the staminate cones by passing it through a 60 to 80 mesh/inch screen. Fresh pollen is generally preferred, and it can be stored with little loss of viability at 0° F. in a desiccator over silica gel for periods up to 1 year.

Red pine pollen will germinate in distilled water. Pollen viability tests using the agar or hanging-drop technique (Wright 1962) are satisfactory. Germination counts also can be made from pollen germinated on the surface of distilled water in sterile, cotton-stopped vials. Germination estimates can be made after 48 to 72 hours at 75° F.

The stages of ovulate cone development presented by Cummings and Righter (1948) are quite satisfactory for red pine. All ovulate cones, even on the same tree, do not reach maximum receptivity at the same time. As it is often impractical to observe and pollinate the cones separately, pollinations are usually made when most of the cones are receptive. The isolation bags usually are left over the cones for 10 to 20 days following pollination. This is undoubtedly longer than necessary, but presence of the bags apparently is not harmful.

During the subsequent 14- to 15-month period, the developing conelets and cones must be protected from cone insects which may be a serious problem, especially in areas where red pine is common. To date satisfactory control of these cone insects has not been attained. One possible exception is where sprinkler heads, with a hose reaching to the ground, have been mounted in the crowns of individual pines. Frequent spraying of the tree crowns during the growing season has resulted in substantial insect control.⁵

Fiberglass screen bags or cloth bags impregnated with DDT or nicotine sulphate and placed over the cones in midsummer of the second year afford good protection from squirrels and prevent seed loss resulting from early cone opening.

Seed Germination and Establishment

Red pine seeds have no dormancy requirements and will germinate whenever environmental conditions are satisfactory. Usually germination occurs in the late spring or early summer when temperatures are at or above 60° F. (Rudolf 1957). Seed germination is best at temperatures between 70 and 86° F. Fall-sown seeds may germinate in the fall (Eliason 1938), and it is possible that some fall germination occurs in the field.

⁵ Correspondence with M. J. Holst, Canada Department Fisheries and Forestry, Jan. 25, 1967, on file at Department of Fisheries and Forestry, Fredericton, New Brunswick.

Although red pine seeds germinate under a wide variety of seedbed conditions, seedling establishment is best on mineral soil, thin grass, or litter under partial shade (Rudolf 1957). Under natural conditions, red pine seedlings become established after fire or other stand disturbances (Spurr 1953; Fowler 1965c). Such disturbances may re-

duce the breeding population to only a few trees which can supply seeds for the area. Fowler (1965 a, c) contends that this method of regeneration results in inbreeding, the rapid elimination of deleterious recessive genes, and tends to reduce the genetic variability of the species.

ASEXUAL REPRODUCTION

In nature, red pine reproduces exclusively by seeds. Natural asexual reproduction has not been reported. Stem cuttings are difficult to root regardless of cultural treatments (Rudolf 1957), and attempts to air-layer this species have been unsuccessful (Hitt 1964).

Rooting

Up to 58-percent rooting of leaf bundles was obtained by Jackalejs (1956) following 24 hours immersion of needle bases in a 10^{-6} M solution of methoxone (2-methyl, 4-chlorophenoxy-acetic acid) and planting at 8 mm. depth in a mixture of coarse sand and peat moss. These rooted bundles failed to develop shoots, but Jackalejs concluded that it should be possible to develop normal plants by using leaf bundles in which buds are already present (resulting from shoot decapitation). He successfully rooted needle bundles from 2- and 7-year-old plants.

Grafting

Grafting has been by far the most successful means of vegetatively propagating red pine. Detailed descriptions of grafting procedures are given by Holst (1956) and Holst, Santon, and Yeatman (1956).

Red pine has been successfully grafted on red pine, Scots pine (*Pinus sylvestris* L.), mugo pine (*Pinus mugo* Turra.), and Japanese red pine (*P. densiflora* Sieb. and Zucc.). It probably can be grafted on any pines of the *Sylvestres* subsection. It also has been grafted on white pine (*P. strobus* L.) and jack pine (*P. banksiana* Lamb.), but resulting grafts are not satisfactory (Ahlgren 1962; Rudolf 1957). Scots pine has been a preferred grafting stock for red pine (Holst 1956) because it is easy to handle in the nursery and greenhouse and because initial grafting success is unusually high.

Incompatibility of scion and stock in interspecific grafts appears to be a serious, although poorly understood, problem with red pine. Holst

(1962) reported 36- to 40-percent graft failure when Scots pine was used as stock following good initial graft success. The incompatibility of stock and scion often does not become evident for several years. Fowler (1967) reported that rooting from the scion occurs when red pine is grafted on Scots pine if the grafts are deep-planted with the scion in contact with the soil. He suggests that this technique could be used to prevent mortality resulting from scion-stock incompatibility. Until more is learned about graft incompatibility, red pine stock is recommended for grafting. There are no reports of intraspecific incompatibility in red pine.

Greenhouse and field grafting of red pine are both successful. The grafting techniques and procedures are similar to those used for other coniferous species. For greenhouse grafting, stock usually is potted about 6 months prior to grafting and vernalized to satisfy dormancy requirements. In southern Ontario, stock brought into the greenhouse in mid-December will break dormancy and grow normally. Grafting should be done after the shoots on the stock plant have begun to elongate.

The choice of grafting method usually is determined as much by the preference of the propagator as by scientific information. The side graft, using dormant scions, is preferred by most propagators and is quite satisfactory (Holst 1956). After grafting, the plants are kept in a high humidity environment from which they are gradually weaned.

In most respects, field grafting using dormant scions is similar to greenhouse grafting. The choice of grafting stock and the techniques are the same. The required high humidity is attained by covering the graft with kraft or polyethylene and kraft bags (Holst 1956). Grafting should not be carried out until shoot elongation has started on the stock plant. Summer field grafting using fresh scions has been used occasionally with red pine. Fowler (1959) reported that up to 96-percent graft success was obtained when fresh scions were cleft grafted and protected with pliofilm and kraft bags, or polyethylene and kraft bags, for 8 to 10 weeks.

Scions of red pine usually are collected during the winter after their dormancy requirements have been satisfied. Holst (1956) found that scions collected from January 15 to March 20, wrapped in polyethylene, and stored at just above or below

freezing temperature were quite satisfactory. Storage of scions for periods of up to 6 months by packing them in snow in a deep freezer (0° F.) has been used successfully for several years by the Ontario Department of Lands and Forests.

GENETICS AND BREEDING

Red pine is the only continental American representative of the widely distributed subsection *Sylvestres*, section *Pinus*, subgenus *Pinus* (Critchfield and Little 1966). Major taxonomic features of red pine are the pink, scaly bark, and long (7 to 17 cm.) needles borne in fascicles of two. The wood is non-resinous and of intermediate density among pines. The karyotype, with a haploid chromosome number of 12, is typical of *Pinus* and is not easily distinguished from karyotypes of other members of the subsection (Saylor 1964).

Morphologically, red pine is an unusually uniform species (Bates 1930; Rudolf 1957; Wright, Bull, and Mitschelen 1963; Fowler 1964a). There are no recognized subspecies, varieties, or forms although individuals with fastigiate branching,⁴ (fig. 4) with unusually slender branches,⁴ and with markedly suppressed lateral branching⁶ are known. Albino or chlorophyll deficient mutant seedlings have been reported with an estimated mutation rate of 0.006 (Wright et al. 1963). Tetraploid seedlings have been noted with a frequency of 0.1 to 0.5 percent in seedling populations.⁴

The existence of only minor inbreeding depression following selfing (Fowler 1965a) indicates that red pine carries relatively few deleterious mutant genes. Self-pollination of 56 trees produced progenies of which only one indicated heterozygosity for a detectable allele in the parent. The low frequency of detectable recessive mutations in red pine suggests that either the mutation rate is low or that mutations are rapidly eliminated. On the assumption that inbreeding plays an important role in natural regeneration of red pine, Fowler (1965b) favors the latter explanation.

Provenance and progeny tests have shown red pine to be one of the least variable species among those for which detailed studies have been carried out. The narrow range of variation suggests that a genetic interpretation of common-environment studies may be more subject to uncertainties associated with nongenetic differences than in most other species. Many existing experiments were established using stock from unreplicated nursery

sowings. Often no information is available on seed weight and growth of the seedlings prior to field planting. Environmental influences known to affect at least early seedling growth are variation in seedbed density (Wright et al. 1963) and variation in fertility of the soil supporting the parental trees (Youngberg 1952). Seed weight was correlated with dry weight of 2-0 seedlings (Hough 1952b), and green weight of seedlings was correlated with height at ages 5 and 10 years (Hough 1957). Fowler (1964a), using several of the provenances studied by Hough (1952 a, b), found that parent-progeny seed weights were unrelated and concluded that differences in seed weight were the result of environmental differences affecting the mother trees. It is clear that further study is needed of the relative proportions of genetic and nongenetic causation of observed variation in red pine. Until such studies are completed, genetic interpretation of provenance and progeny tests will not be conclusive.

In provenance tests relatively small, though statistically significant, differences among provenance means have been reported for survival (Rudolf 1947; Benzie 1958), phenological traits (Rudolf 1954; Rehfeldt and Lester 1966), dimensional traits (Hough 1952a; Sweet 1963; Wright et al. 1963; Holst 1964a; Nienstaedt 1964; Lester 1964; Lester and Barr 1965), photoperiodic response (Vaartaja 1962), lammas frequency (Lester and Rehfeldt 1967), and wood quality (Rees and Brown 1954; Schumann 1960; Peterson 1966). Significant differences among means of one-parent progenies have been reported for dimensional traits (Lester and Barr 1965). In general, the difference between the overall mean and the mean of the best provenance or progeny has been about 10 percent for height growth of plantations up to 20 years. Differences have been greater for very young seedlings (Wright et al. 1963; Fowler 1965a), and somewhat less for older materials (Nienstaedt 1964; Rudolph 1947).

Clinal variation is only weakly indicated in red pine. From northern seed sources, seeds may be smaller (Rudolf 1947), seedlings may have fewer cotyledons (Fowler 1964a), lammas frequency may be less (Lester and Rehfeldt 1967).

⁴ R. G. Hitt, unpublished data, on file at Department of Forestry, University of Wisconsin, Madison, Wis., Sept. 7, 1957.



and frost sensitivity is generally less (Bates 1930; Rudolph 1949; Holst 1962). In a study by Sweet (1963), age-6 height correlated at 0.87 with mean annual temperature and at 0.90 with annual number of days having mean temperature above 45° F. Hough (1952a), Rudolf (1964), and Wright et al. (1963) have demonstrated differences between provenances from different climatic regions in respect to several attributes (notably height growth). Variation between provenances within climatic regions is also present (Wright et al. 1963). Holst (1964b), considered the variation pattern of red pine to be predominantly random from stand to stand, especially in western Ontario where occurrence of the species is spotty.

Genetic variation induced by interspecific hybridization with red pine has been nearly impossible to obtain because of strong barriers to crossing. Of the many hybridization attempts in the United States and Canada, only one cross, *Pinus nigra* var. *austriaca* (Hoess) Aschers, and Graebn. X *P. resinosa* in California, has yielded verified interspecific hybrids (Duffield & Snyder 1958; Richter 1962; Critchfield 1963). Critchfield suggested that the successful cross may have resulted from accidental contamination of red pine pollen with Austrian pine pollen. Pollen mixes using pollen of both species subsequently have been tried in California, Ontario, and Wisconsin. Pollen mixes using red pine and other *Sylvestres* pines have been tried in Ontario (Fowler 1964c). These crosses failed to produce any verified hybrids.^{7, 8} One attempt to repeat the original cross with uncontaminated pollen, and several attempts to backcross the hybrids to red pine also have been unsuccessful. By contrast, the hybrids have been successfully backcrossed (mean 4.4 germinable seeds per cone) to Austrian pine.⁷

In summary, significant natural variation between provenances and one-parent progenies of red pine has been demonstrated for many of the characteristics studied. For most characteristics, the pattern of variation is obscure. Clinal variation in response to environmental gradients based on available climatic data are weak. Variation among progenies and provenances within climatic regions appears to be as great as variation between regions. Nongenetic effects may bias a genetic interpretation of observed variation.

⁷ Correspondence with W. B. Critchfield, USDA Forest Service, Institute of Forest Genetics, Placerville, Calif., Feb. 21, 1967, on file at Department of Fisheries and Forestry, Fredericton, New Brunswick.

⁸ Correspondence with C. C. Heimbürger, Ontario, Department Lands and Forests, Maple, Ontario, Mar. 14, 1967, on file at Department of Fisheries and Forestry, Fredericton, New Brunswick.

Figure 4.—Red pine showing fastigiate branching, Buckatabon, Wis. (Photo by University of Wisconsin, Madison.)

The usefulness of observed variation in red pine for genetic improvement is questionable. Fowler (1964d) concluded that the probability of genetic improvement through seedling or clonal seed orchards is negligible. Rudolf (1964) suggested that there is some possibility for improvement, while Nienstaedt (1964), Lester (1964, 1965), and Holst

(1964b) concluded that worthwhile improvement is possible. Dominance variance seems of minor importance in red pine (Fowler 1965a) and so the crux of the problem is the separation of additive genetic variance from nongenetic environmental effects, including maternal effects reported by Fowler (1965a).

IMPROVEMENT PROGRAMS

The feasibility of programs for genetic improvement in red pine is largely contingent on incorporation of small amounts of genetic gain in large numbers of seedlings. This restricts such programs to areas where the species is a major part of large reforestation efforts (Ontario, Michigan, Wisconsin). Lundgren and King (1965) presented hypothetical examples of improvement programs in which small genetic gains in height growth of red pine gave modest financial rates of return on program costs. Data on variation in growth rate in young progeny tests, if applicable to performance at rotation age, indicate potential genetic gains of the magnitude necessary to make a breeding program economically justifiable if red pine is widely planted (Lester 1965).

In much of the area where red pine is planted, increased volume growth is an obvious major objective of breeding. Increasing pulpwood demands and trends toward homogenization of wood favor a long term goal of increased production of wood substance per acre per year. The absence of a strongly negative association between radial growth rate and specific gravity (Peterson 1966) suggests that increased volume growth will represent proportionate increases in wood yields.

Although red pine is relatively free from major insect and disease problems over much of its commercial range, attack by European pine shoot moth is a serious threat to plantation establishment and to growth of established plantations on poor or fair sites (Heikkinen and Miller 1960). Holst (1963) has observed that chances for selection of resistant trees seem slight. The apparent relationship between vigor and susceptibility to attack (Heikkinen and Miller 1960) suggests that restricting the planting of red pine to the better sites may be a more promising approach than intraspecific selection and breeding. An interspecific approach to resistance is difficult because of the crossing barrier between red pine and other pines. If this barrier can be overcome, interspecific hybridization may be a promising source of variation for resistance breeding (Critchfield 1963).

In considering alternative approaches to genetic

improvement, available evidence directs the tree breeder toward a program of intraspecific selection at either the population or individual tree level. Although provenance hybridization may have some promise, the apparent paucity of dominance variance would seem to restrict genetic approaches to schemes emphasizing additive genetic variance. In the absence of information on the relative contributions of provenances, stands within provenances, and individuals within stands to total genetic variance, the most efficient approach to selection is not determinable.

Data from young provenance tests indicate that provenance selection might give worthwhile gains particularly in view of some evidence for an association between rate of height growth and length of growing season (Sweet 1963; Wright et al. 1963). Variation between seed collections from stands within a climatic region also may be appreciable, at least in areas like western Ontario where stands often are well isolated from each other (Holst 1964b). Determining whether stand to stand differences are primarily attributable to genetic or nutritional differences may be a problem (Youngberg 1952). Variation in progeny means from individual trees also can be substantial and comparable in magnitude to variation between provenance means (Lester and Barr 1965).

Studies now in progress (Wright 1964b; Holst 1964b; Lester 1965) will contribute much to knowledge of population structure. Each of the cited studies, however, is based on open-pollinated, one-parent progenies. Further investigation of the possible maternal effects discussed by Fowler (1965a) will be needed before an unequivocal genetic interpretation of these studies can be accepted. At least until the necessary clarification of genetic and nongenetic causes of variation is available, individual tree selection is probably the most promising approach to genetic improvement in red pine. In many areas, extensive natural stands or relatively uniform sites are unavailable, but selection can be accomplished in fast growing plantations. The need for progeny testing is explicit in all recent discussions of genetic improvement in red pine.

Selection standards for red pine have not been developed. Wright and Bull (1963) suggested that information on inheritance was inadequate to show what traits should be selected for efficient genetic gain. King,⁹ using data from 34 red pine stands in the Great Lake States, suggests that one simple criterion could be selection of vigorous, well-formed, disease-free trees having a crown volume/stem volume ratio of less than one-third of the mean for dominant and codominant trees in each stand.

Several factors combine to make the progeny test-seedling seed orchard approach attractive as a starting point. The necessity for large-scale progeny testing, the apparent absence of appreciable dominance variance, anticipated commercial seed

production by age 20 to 25, and moderate rotation ages of 50 to 80 years for the predominant uses of red pine are major considerations. Availability of relatively uniform sites is also relevant.

Current projects (Wright 1964b; Lester 1965) on genetic improvement of red pine have dual objectives: Production of genetic information, and production of commercial quantities of seed incorporating some genetic improvement. Genetic gains are to be obtained through combined family and within-family selection among open-pollinated progenies. Thinnings between ages 10 and 30 are expected to remove about 95 percent of each progeny test, leaving a breeding population from which to obtain genetically improved seed as well as a base population for further genetic advances.

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